



Extinction-driven changes in frugivore communities on oceanic islands

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Extinction-driven changes in frugivore communities on oceanic islands

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Global change and human expansion have resulted in many species extinctions worldwide, but the geographic variation and determinants of extinction risk in particular guilds still remain little explored. Here, we quantified insular extinctions of frugivorous vertebrates (including birds, mammals and reptiles) across 74 tropical and subtropical oceanic islands within 20 archipelagos worldwide and investigated extinction in relation to island characteristics (island area, isolation, elevation and climate) and species' functional traits (body mass, diet and ability to fly). Out of the 74 islands, 33 islands (45%) have records of frugivore extinctions, with one third (mean: 34%, range: 2–100%) of the pre-extinction frugivore community being lost. Geographic areas with more than 50% loss of pre-extinction species richness include islands in the Pacific (within Hawaii, Cook Islands and Tonga Islands) and the Indian Ocean (Mascarenes, Seychelles). The proportion of species richness lost from original pre-extinction communities is highest on small and isolated islands, increases with island elevation, but is unrelated to temperature or precipitation. Large and flightless species had higher extinction probability than small or volant species. Across islands with extinction events, a pronounced downsizing of the frugivore community is observed, with a strong extinction-driven reduction of mean body mass (mean: 37%, range: –18–100%) and maximum body mass (mean: 51%, range: 0–100%). The results document a substantial trophic downgrading of frugivore communities on oceanic islands worldwide, with a non-random pattern in relation to geography, island characteristics and species' functional traits. This implies severe consequences for ecosystem processes that depend on mutualistic plant–animal interactions, including ecosystem dynamics that result from the dispersal of large-seeded plants by large-bodied frugivores. We suggest that targeted conservation and rewilding efforts on islands are needed to halt the defaunation of large and non-volant seed dispersers and to restore frugivore communities and key ecological interactions.



Introduction

Global biodiversity is decreasing at an alarming rate (Ceballos et al. 2017). Extinction rates of species are currently at least 100 times higher than the 'background' rate from the fossil record (Ceballos et al. 2015) and many plants and animals show extirpations and severe declines in species abundance (Butchart et al. 2010, Dirzo et al. 2014). Extinction is a selective process because both extrinsic and intrinsic factors result in a non-random loss of species (Blackburn et al. 2004, Cardillo et al. 2005, Boyer and Jetz 2010, 2014). For instance, extrinsic factors such as small area size, low rainfall and high elevation can increase species extinction risk on islands (MacArthur and Wilson 1967, Blackburn et al. 2004, Duncan et al. 2013). On the other hand, intrinsic factors such as species traits can determine extinction risk, e.g. large-bodied, flightless or specialized species might be more prone to extinction than small-bodied, volant or generalist species (Cardillo et al. 2005, Estes et al. 2011, Duncan et al. 2013, ESKILDSEN et al. 2015). These non-random extinctions can have severe consequences for ecosystem processes, e.g. when extinction-driven body-size reduction results in the downsizing and trophic downgrading of communities (Galetti et al. 2013, Pérez-Méndez et al. 2015, 2016, Svenning et al. 2016).

Islands tend to have lower species richness, more endemic species, and more pronounced extinction rates than mainland ecosystems (Whittaker and Fernandez-Palacios 2007, Hansen and Galetti 2009, Kier et al. 2009, Whittaker et al. 2017). This is partly due to their isolation and small size which accommodates a limited number of species and facilitates the evolution of unique species interactions (MacArthur and Wilson 1967, Kaiser-Bunbury et al. 2010, Lomolino et al. 2010). It makes island biota particularly vulnerable to global change, e.g. related to human colonization, habitat degradation, hunting and invasive species (Whittaker and Fernandez-Palacios 2007). As a consequence, many species have gone extinct on islands worldwide, especially on oceanic islands (Blackburn et al. 2004, Steadman 2006, Hansen and Galetti 2009, Duncan et al. 2013, Boyer and Jetz 2014, Whittaker et al. 2017). The loss of these species from island ecosystems also means a loss of interactions among species, such as those between plants and frugivores (Meehan et al. 2002, Kaiser-Bunbury et al. 2010, Pérez-Méndez et al. 2015, 2016).

Plant–frugivore interactions are important for the resilience of ecosystems to global change because frugivores disperse the seeds of many plants and thereby contribute to reproductive success, colonization ability and genetic structure of plant populations (Nathan and Muller-Landau 2000, Nathan 2006, Pérez-Méndez et al. 2015, 2016). This is particularly true in the tropics and subtropics where many vertebrates include fleshy fruits in their diet and up to 90 percent of all shrubs and trees depend on animal-mediated seed dispersal (Fleming et al. 1987, Fleming and Kress 2013). Specialized frugivores (i.e. obligate fruit eaters) are strictly tropical/subtropical in their distribution (Kissling et al. 2009) and some specific groups of birds (e.g. fruit pigeons) and volant mammals (e.g. fruit bats) are of key importance

for long-distance dispersal of plants, e.g. for the colonization of oceanic islands (Whittaker and Jones 1994, Nathan 2006). Moreover, large-bodied frugivorous birds such as pigeons or flightless birds such as the dodo (Meehan et al. 2002, Hansen and Galetti 2009, Wotton and Kelly 2012) as well as reptiles such as lizards and tortoises are especially relevant for seed dispersal on islands (Olesen and Valido 2003, Blake et al. 2012, Hansen and Traveset 2012). Hence, on islands all three vertebrate groups (birds, mammals and reptiles) are important seed dispersers, and the particular traits of frugivores (e.g. flight ability and body mass) might play an important role for seed dispersal.

Here, we quantify extinction-driven changes of insular frugivore communities on 74 islands within 20 archipelagos worldwide. We focus on oceanic islands in the tropics and subtropics because 1) seed dispersal by vertebrates is most prevalent in the (sub)tropics (Kissling et al. 2009), and 2) oceanic islands are of particular conservation concern due to their unique biota, high levels of endemism as well as high rates of biodiversity loss (Blackburn et al. 2004, Kier et al. 2009, Kaiser-Bunbury et al. 2010, Whittaker et al. 2017). We determine the magnitude of frugivore extinctions (including birds, mammals and reptiles) and explore how it varies with extrinsic and intrinsic factors, i.e. with island characteristics (island area, isolation, elevation and climate) and species' functional traits (body mass, diet and ability to fly). First, we ask to what extent insular frugivore extinctions vary geographically, expecting that islands in the Pacific are most strongly affected because they have at least two waves of anthropogenic extinctions of the native fauna, one related to pre-European colonization about 1600 yr ago (i.e. seafaring Polynesians) and one after European contact in the 18th century (Steadman 2006, Boyer 2008, Duncan et al. 2013, Boyer and Jetz 2014). Second, we test whether the proportional extinction of frugivores could be explained by key island characteristics, especially by small island area, large isolation, low rainfall and high elevation (MacArthur and Wilson 1967, Blackburn et al. 2004, Whittaker and Fernandez-Palacios 2007, Duncan et al. 2013). Third, we quantify whether extinction probability can be predicted with functional traits of frugivores, e.g. that large and flightless species are most prone to extinctions (Cardillo et al. 2005, Hansen and Galetti 2009, Boyer and Jetz 2010, 2014). Fourth, we ask how extinction affects the frequency distributions of body masses within insular frugivore communities, expecting an ecological downsizing and body-size reduction at the community level that results from the predominant loss of large-bodied species (Estes et al. 2011, Dirzo et al. 2014, Pérez-Méndez et al. 2015).

Material and methods

Frugivore occurrences on islands

We collected species occurrences of extant and extinct frugivorous vertebrates (incl. birds, mammals and reptiles)

for 74 tropical and subtropical oceanic islands within 20 archipelagos worldwide. We refer to the frugivore assemblage on an island as ‘community’. Our focus was on tropical or subtropical regions where seed dispersal by frugivorous vertebrates is most pronounced (Howe and Smallwood 1982, Kissling et al. 2009) and conservation concern about the loss of frugivores particularly high (Kaiser-Bunbury et al. 2010). We further focused on oceanic islands because they have formed over oceanic plates with phases of emergence, development, and submergence, and have never been connected to continental landmasses (Whittaker and Fernandez-Palacios 2007, Whittaker et al. 2017). Oceanic islands are more isolated than continental ones (Weigelt et al. 2013) and consequently have high levels of endemism (Kier et al. 2009) with a large number of documented extinctions since human contact (Blackburn et al. 2004, Steadman 2006, Duncan et al. 2013, Whittaker et al. 2017). We also included four granitic islands in the Seychelles which are considered para-oceanic islands, i.e. comparatively small islands of a continental origin that behave like oceanic ones in terms of distance to the mainland and a long-term isolation (Kaiser-Bunbury et al. 2010).

The islands were distributed across the Pacific, Atlantic and Indian Ocean. We included resident species but excluded non-native and vagrant species as well as migrants and non-breeding visitors. Occurrence data was compiled from a comprehensive literature search including scientific articles, books, monographs, inventory lists, fossil descriptions and other sources (Supplementary material Appendix 1). Literature was searched systematically by using keywords such as ‘extinct’ or ‘frugivore’ and with specific names of island or species.

We generally included all species that have fruit in their diet. For extant species this information was derived from books and published databases (Kissling et al. 2009, 2014, Del Hoyo et al. 2011), complemented with systematic literature searches for particular species (Supplementary material Appendix 1). For extinct species, frugivory was assessed with diet descriptions from the literature, often based on morphological and dental analyses. In some cases, frugivory had to be estimated from the closest taxonomic relative. A detailed overview of the diet collection and literature sources is provided in Supplementary material Appendix 1.

Island characteristics

For each island, we defined the spatial extent using island polygons from the Global Administrative Areas (GADM) database ver. 2.8 (< www.gadm.org/ >). We extracted data on island characteristics including area (km²), isolation distance from the nearest mainland (km), maximum elevation (m), annual precipitation (mm), surrounding landmass proportion (log₁₀ proportion) and annual mean temperature (°C). These data were obtained from a standardized dataset on environmental characterization of the world’s islands (Weigelt et al. 2013). As measures of isolation we included both distance to the nearest mainland (DIST) and surrounding landmass proportion (SLMP) because they represent different aspects of isolation (Weigelt and Kreft 2013). DIST represents the shortest distance from an island to the nearest mainland and is typically used in studies of island biogeography (MacArthur and Wilson 1967, Whittaker and Fernandez-Palacios 2007, Whittaker et al. 2017). SLMP characterizes the amount of land area surrounding the target island and has been shown to be a key predictor of insular plant diversity (Weigelt and Kreft 2013).

Functional traits

For all extant and extinct frugivores, we collected information about three functional traits that are important for seed dispersal: body mass (continuous, in g), amount of fruit in the diet (categorical: low, medium or high) and ability to fly (categorical: volant vs non-volant). These trait data were obtained using a range of different methods, including calculations, available databases, estimates, genus means, primary literature, morphology or surrogate species. A summary of methods for the three functional traits is provided in Table 1.

Body mass data were mostly obtained from existing databases (Table 1), including birds (Dunning 2008), mammals (Sandom et al. 2013) and reptiles (Meiri 2010). Additionally, the primary literature was searched for body mass values or to estimate body mass from literature (Supplementary material Appendix 1). For about a quarter of the species, body mass data had to be approximated by the genus mean (i.e. mean value across species within the same genus) or

Table 1. Percent use of methods to collect information on traits (body mass, amount of fruit in diet, flight ability) for extant and extinct frugivorous vertebrates (birds, mammals, reptiles) on islands worldwide. Percentages reflect how often a particular method has been used to derive information on a particular trait across all included vertebrates (n = 387 species).

Method	Explanation	Body mass	Diet	Flight ability
Calculation	Calculated using equations for morphometrics (only for body mass)	9	0	0
Database	Directly obtained from available databases (body mass and diet)	60	58	0
Estimate	Estimates supported by literature (body mass and diet)	4	19	0
Genus mean	Mean value across species within the same genus (all traits)	13	7	1
Literature	Directly obtained from individual articles (all traits)	3	14	5
Morphology	Evaluated on the basis of morphological characteristics (only flight ability)	0	0	94
Surrogate	Surrogate data from taxonomically related, morphologically similar species (body mass and diet)	11	2	0
Total %		100	100	100

by surrogate species (i.e. using data from taxonomically related and morphologically similar species) because species-specific body mass values were missing. For some species (e.g. many reptiles), body mass was calculated using published morphometric data together with allometric equations (Pough 1980) using family-specific slopes (Meiri 2010). For tortoises, body mass was calculated with morphometric data from 182 Aldabra giant tortoises (*Aldabrachelys gigantea*) (Supplementary material Appendix 2).

The amount of fruit in the diet of each of the species was predominantly derived from existing databases (Kissling et al. 2009, 2014), but also from the primary literature, genus means or surrogate species (Table 1). Because the diet of extinct species could not be quantified at the same level of detail as the diet of extant species, we used three categories to harmonize diet estimates across species and vertebrate classes: low ($\leq 30\%$), medium (40–60%) or high (70–100%) amounts of fruit in the diet. For birds, we used the proportion of fruits in the diet (Kissling et al. 2009) relative to other dietary components mentioned in the literature (Del Hoyo et al. 2011). For mammals, we used the MammalDIET database (Kissling et al. 2014) and assigned data from rank 1, rank 2 and rank 3 as high, medium and low amounts of fruit, respectively. For reptiles as well as mammal and bird species without diet information from existing diet databases, additional primary literature, books and websites (Supplementary material Appendix 1) were used to assign the most likely diet category. In case species-specific diet descriptions were not available, the diet of close taxonomic relative(s) or the genus mean from existing databases (Kissling et al. 2009, 2014) was used as a surrogate.

The ability to fly was recorded as a binomial trait (volant or non-volant), mostly evaluated on the basis of morphological characteristics as well as descriptions from books and the primary literature (Table 1; Supplementary material Appendix 1). All reptiles and rodents were assigned to the non-volant category and all fruit bats to the volant category. For birds, the ability to fly was evaluated separately for each species by considering their morphology (e.g. with the help of images). Additional literature was searched for extinct bird species, for bird species which belong to a taxonomic group with several known flightless species (e.g. rails, pigeons, megapodes), or when wings were absent or small.

An overview of all trait data sources is provided in Supplementary material Appendix 1. Moreover, the species-specific trait data, the methods used, and specific sources for each species are available as a dataset from the Dryad Digital Repository.

Analysis

Four aspects of extinction-driven changes in insular frugivore communities were investigated: 1) geographic variation in the extent of insular frugivore extinctions, 2) the relationship between the proportion of frugivore extinctions and key island characteristics, 3) the relationship between

extinction probability and functional traits, and 4) ecological downsizing, i.e. community-level body-size reduction due to extinctions.

In a first step, we quantified the magnitude of extinction on each island by calculating the species richness of the pre-extinction community (sum of extant and extinct species richness) as well as their proportional extinction (number of extinct species divided by the pre-extinction species richness).

In a second step, we assessed the relationship between proportional extinction and six island characteristics (area, distance from mainland, maximum elevation, annual precipitation, surrounding landmass proportion, and mean temperature) using a generalized linear mixed effects model (GLMM) with a binomial error distribution and a logit link function, following the guidelines of Zuur et al. (2009). Proportional extinction was used as the response variable and pre-extinction species richness as a weight. The weight defines the variance structure of the GLMM by dividing the scale parameter of the model with the weight values for each island. The six island characteristics were used as predictor variables. They were not strongly correlated with each other (all Spearman rank correlations $r < 0.6$), scaled with a Z-transformation, and included as fixed effects in the GLMM. We further accounted for the nestedness of islands within archipelagos by using archipelago ($n=20$) as a random effect for the intercept. Following Nakagawa and Schielzeth (2013), we calculated the marginal R^2 to quantify the variance explained by fixed factors, and the conditional R^2 to quantify the variance explained by both fixed and random factors.

In a third step, we used a GLMM with a binomial error distribution and a logit link function to test the relationship between extinction status and functional traits (body mass, amount of fruit in the diet, and ability to fly). We used the binary extinction status (extinct=1, extant=0) for a specific species on a specific island as response variable (i.e. island populations). This included a total of 1185 extinct and extant species occurrences (extinct: 122, extant: 1063) because the same species might be extinct and/or present on different islands. This way of implementation does not account for the independence of species, but we additionally tested species-level analysis by calculating the proportion of islands where each species went extinct. This alternative implementation (using species rather than island populations as the unit of analysis) yielded similar results, so we only present the analysis at the level of island populations. In this analysis, both body mass and amount of fruit in the diet were used as predictor variables. Body mass was scaled with a Z-transformation. To correct for taxonomic nestedness of species, we used taxonomic class (bird, mammal or reptile) as a random effect for the intercept in the GLMM. We further included ability to fly (yes=1, no=0) as a random effect within each taxonomic class.

In a fourth step, we assessed ecological downsizing by quantifying extinction-driven changes in community-level

mean and maximum body mass for all islands with recorded extinction events ($n=33$). Changes in mean body mass (g) were calculated by subtracting the post-extinction mean (using extant species) from the pre-extinction mean (using extant and extinct species). We then divided the change in body mass by the pre-extinction mean body mass to obtain the proportional change in body mass. The change in maximum body mass was calculated in a similar way. Body mass frequency distributions were visualized with horizontal density strips and data were log-transformed before calculations.

All statistical analyses were done with the R software ver. 3.2.5 (R Development Core Team). For quantifying the magnitude of extinctions (step 1) we used R packages 'ggplot2' and 'ggmap'. For the GLMMs (steps 2 and 3), we used the R packages 'lme4' and 'lmerTest'. We further employed a stepwise model selection based on Akaike information criterion corrected for small sample sizes (AICc) using the R package 'MuMIn'. GLMMs with a $\Delta\text{AICc} \geq 4$ compared to the best model were rejected (Burnham and Anderson 2002). For the first GLMM analysis (step 2), this resulted in eight GLMMs with similar support. We therefore used model averaging (R function 'model.avg()') to obtain a final model. For the second GLMM analysis (step 3), no model averaging was needed because only one GLMM had $\Delta\text{AICc} < 4$. Finally, for visualizing changes in body mass frequency distributions (step 4) the R package 'denstrip' was used.

Data deposition

Data available from the Dryad Digital Repository: < <http://dx.doi.org/10.5061/dryad.s522m> > (Heinen et al. 2017).

Results

Magnitude and geographical distribution of insular frugivore extinctions

The 74 studied islands covered a size range of 5–5000 km², and included oceanic islands in all three major oceans (Fig. 1). Of those islands, 33 (45%) showed ≥ 1 recorded frugivore extinction (Fig. 1, Supplementary material Appendix 3). For those 33 islands, the proportion of species richness lost from the original frugivore communities was 34% (median: 18%), ranging from 2% on the Solomon islands Choiseul and Malaita to 100% on the Hawaiian islands Ohau and Lanai. Insular frugivore extinctions varied geographically, with Hawaii, the Cook Islands, Tonga Islands, the Mascarenes and the Seychelles being those archipelagos that are most affected (all containing islands with proportional extinctions ≥ 0.5 ; Fig. 1). Hence, Pacific islands show the highest proportions of frugivore extinctions worldwide, but high proportional extinctions were additionally recorded in parts of the Indian Ocean (Mascarenes and Seychelles).

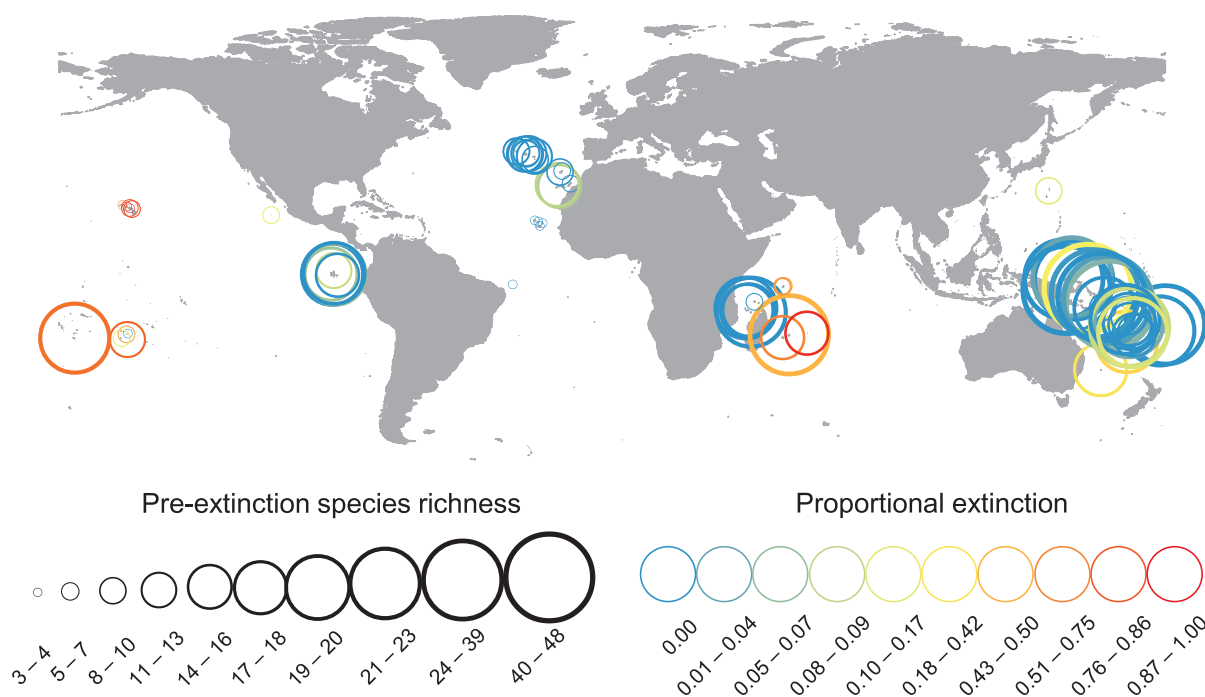


Figure 1. Geographic variation of insular frugivore extinctions across 74 islands worldwide. Pre-extinction species richness of frugivores is illustrated by circle size (using quantile classification), with larger circles showing islands with more species. Proportional extinction reflects the relative number of species lost from the original frugivore communities, illustrated with colors ranging from blue (no extinctions) to orange and red (high proportional extinctions). Only native fruit-eating vertebrate species (birds, mammals, reptiles) are included. The circles are plotted for the mass centroid of each island using the World Geodetic System 1984 (WGS 84) as the geographic coordinate system.

Across all islands ($n=74$), proportional extinction was only weakly (and negatively) correlated with pre-extinction species richness (Spearman rank: $r=-0.11$), but for the subset of islands with extinction events ($n=33$) this correlation was strong (Spearman rank: $r=-0.70$), indicating that species-rich islands tend to have lower proportional extinctions than species-poor islands.

Extinction and island characteristics

Model averaging of eight GLMMs with similar support (Supplementary material Appendix 4) revealed that three island characteristics were particularly important to explain proportional extinction: island area, distance to mainland, and elevation (Fig. 2). The most important factor was distance to mainland (Fig. 2a), with proportional extinction increasing the further away islands are from the mainland (Fig. 2c). Island area was the second most important factor (Fig. 2a), with small islands having large proportional extinction (Fig. 2b). Maximum elevation of islands also showed a statistically significant effect, with low elevation islands having less proportional extinction (Fig. 2d). Other

factors such as surrounding landmass proportion, temperature and precipitation did not play an important role in explaining proportional extinction. Hence, the hypothesis that small island area, large isolation, and high elevation could explain the magnitude of insular extinctions was supported, but climate variables did not play an important role. Furthermore, variance partitioning showed that variation among archipelagos dominates: the marginal R^2 values (fixed factors only) for the eight models with similar support (Supplementary material Appendix 4) were around 0.25, while the conditional R^2 values (both fixed and random factors) were around 0.65.

Traits and extinction probability

The best GLMM to explain extinction probability of 1063 extant and 122 extinct occurrences of 378 unique frugivorous species was a model that included body mass as a fixed effect and ability to fly (volant or non-volant) and taxonomic class (bird, mammal, reptile) as random effects (Fig. 3). This model was better ($\Delta AIC_c > 4$) than GLMMs using diet or no fixed effects (Supplementary material Appendix 5)

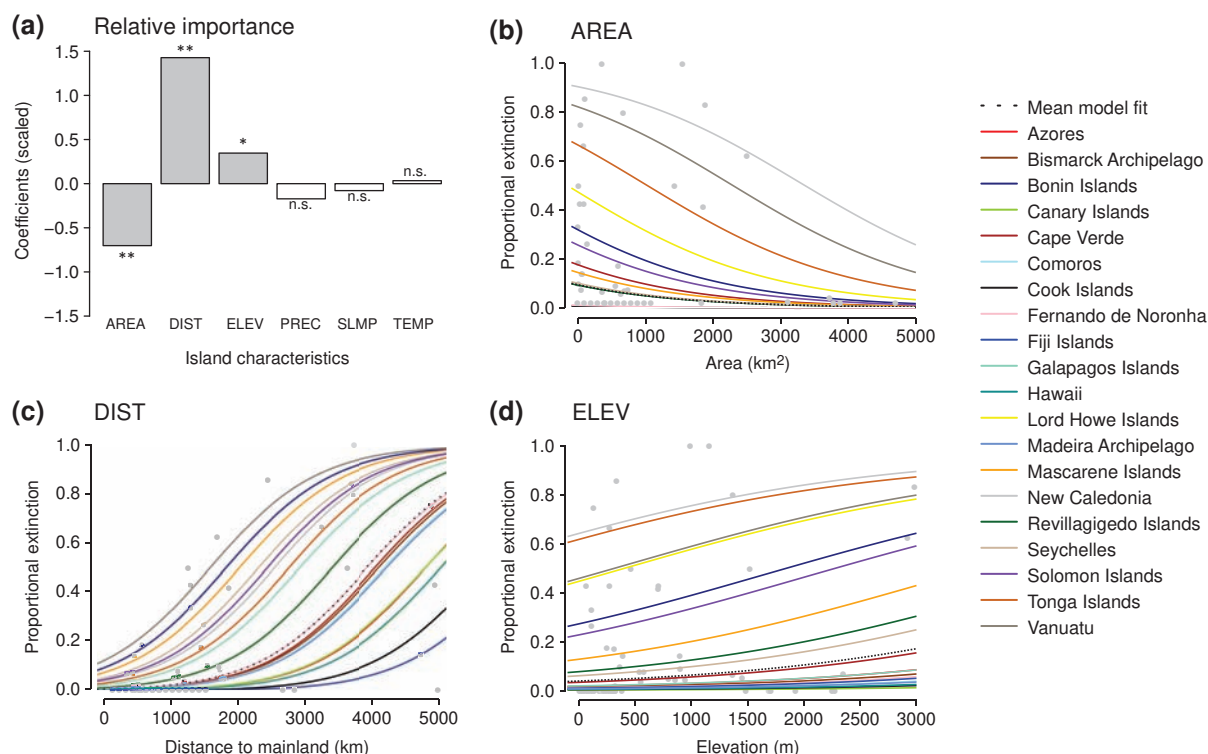


Figure 2. The effect of island characteristics on frugivore extinctions across 74 islands worldwide. (a) Relative importance of predictor variables as indicated by the strength of coefficients (grey=statistically significant predictors, white=not significant). (b–d) Relationship between proportional extinction and island area, distance to mainland, and maximum elevation, respectively. Results were obtained from model averaging of eight generalized linear mixed effects models with similar support (Supplementary material Appendix 4). The proportion of extinct frugivores (birds, mammals, reptiles) was used as response variable and six island characteristics as predictors (scaled before analysis). The model was weighted with pre-extinction species richness. Archipelago was used as a random effect on the intercept (reflected with colored lines in b–d). Abbreviations of island characteristics: AREA=island area (km²); DIST=distance to mainland (km); ELEV=maximum elevation (m); PREC=annual precipitation (mm yr⁻¹); SLMP=surrounding landmass proportion (log₁₀ proportion); TEMP=annual mean temperature (°C).

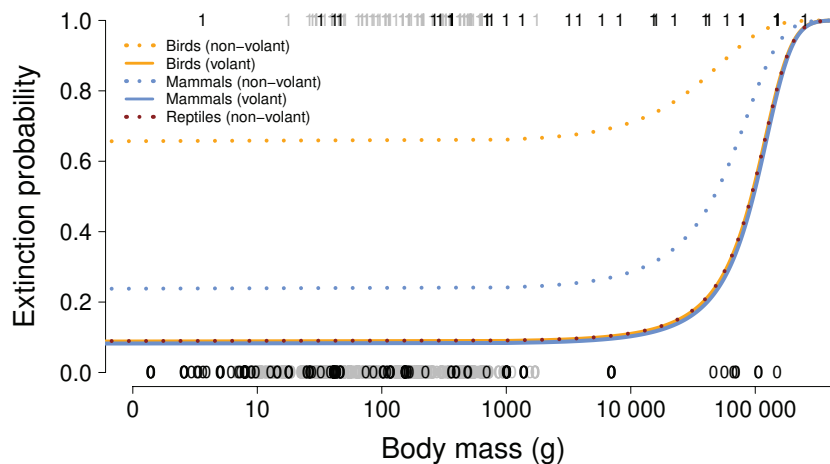


Figure 3. Extinction probability of frugivorous birds, mammals and reptiles in relation to body mass and ability to fly. For all taxa, the probability of extinction increases with large body mass (logarithmic x-axis, in g), but extinction is higher for non-volant birds and mammals compared to volant species. Results are obtained from a binomial generalized linear mixed effects model (GLMM) with body mass as a fixed effect and the ability to fly (volant, non-volant) and taxonomic class (bird, mammal, reptile) as random effects (compare Supplementary material Appendix 5). The GLMM was based on 1185 species occurrences of 387 unique species on 74 islands. The body masses of extinct species are plotted as '1' and those of extant species as '0', with black indicating non-volant species and grey representing volant species.

and revealed that extinction probability is particularly high for large-bodied species (Fig. 3). Moreover, for birds and mammals it showed that extinction probability depends on the ability to fly, with non-volant species having a higher probability of going extinct than volant species (Fig. 3). This supported the hypothesis that large and flightless species are most prone to extinctions.

Downsizing and changes in community-level body mass

For most of the 33 islands with recorded extinction events, the loss of species resulted in a downsizing of the frugivore community (Fig. 4). On average, extinctions decreased community-level mean body mass by one third (mean: 37%, range: -18–100%) relative to the pre-extinction community. The two Hawaiian islands Oahu and Lanai showed a complete loss of their native frugivore community (Fig. 4). In contrast, three islands in the Pacific (Rarotonga of Cook Islands, Ambrym of Vanuatu, and Santa Cruz of Galapagos) surprisingly showed a slight increase in community-level body mass because the extinct frugivores were smaller in body size than the community mean (Fig. 4). Nevertheless, all other 30 islands showed a decrease in community-level body mass indicating ecological downsizing (Fig. 4). Across islands, the largest species (> 1.2 kg) that were lost were reptiles and birds (Fig. 4). These included tortoises (order Testudines) such as species in the genera *Chelonoidis*, *Cylindraspis* and *Meiolania*, as well as scaled reptiles (order Squamata) such as giant lizards and skinks, e.g. the goliath Tenerife lizard *Gallotia goliath* and the Mauritian giant skink *Leiolopisma mauritiana*. For birds, this included flightless ducks (order Anseriformes), pigeons (order Columbiformes) and wildfowl (order Galliformes) such as the giant *Sylvionis neocaledoniae*

from New Caledonia, the Rodrigues solitaire *Pezophaps solitaria*, the dodo *Raphus cucullatus* from Mauritius, and a large goose-like duck (*Thambetochen chauliodous*) from the Hawaiian Islands.

Compared to the mean body mass changes at the community-level, the changes in the largest (heaviest) species were often pronounced. Across the 33 islands, the maximum body mass of post-extinction frugivore communities was severely reduced (mean = 51%, range: 0–100%) when compared to the pre-extinction communities. On about one third (11 of 33) of the islands, the maximum body mass did not change (i.e. the largest species is still present). However, most of them still showed an ecological downsizing, i.e. a decrease in community-level mean body mass (due to the loss of species with a body mass larger than the pre-extinction community-level mean). Overall, our results document a pervasive ecological downsizing and body-size reduction of insular frugivore communities. However, they also provide hope because some large-bodied species are still left, at least on some islands.

Discussion

Our study provides a first comprehensive overview of frugivore extinctions on oceanic islands worldwide. The results show that losses of frugivorous species have been reported on almost half of the 74 studied islands, and that on average about one third of the original community has disappeared. We further show that both extrinsic factors (e.g. physical conditions such as island size, isolation and archipelago membership) and intrinsic traits (e.g. large body size and inability to fly) are key predictors of extinction risk, and

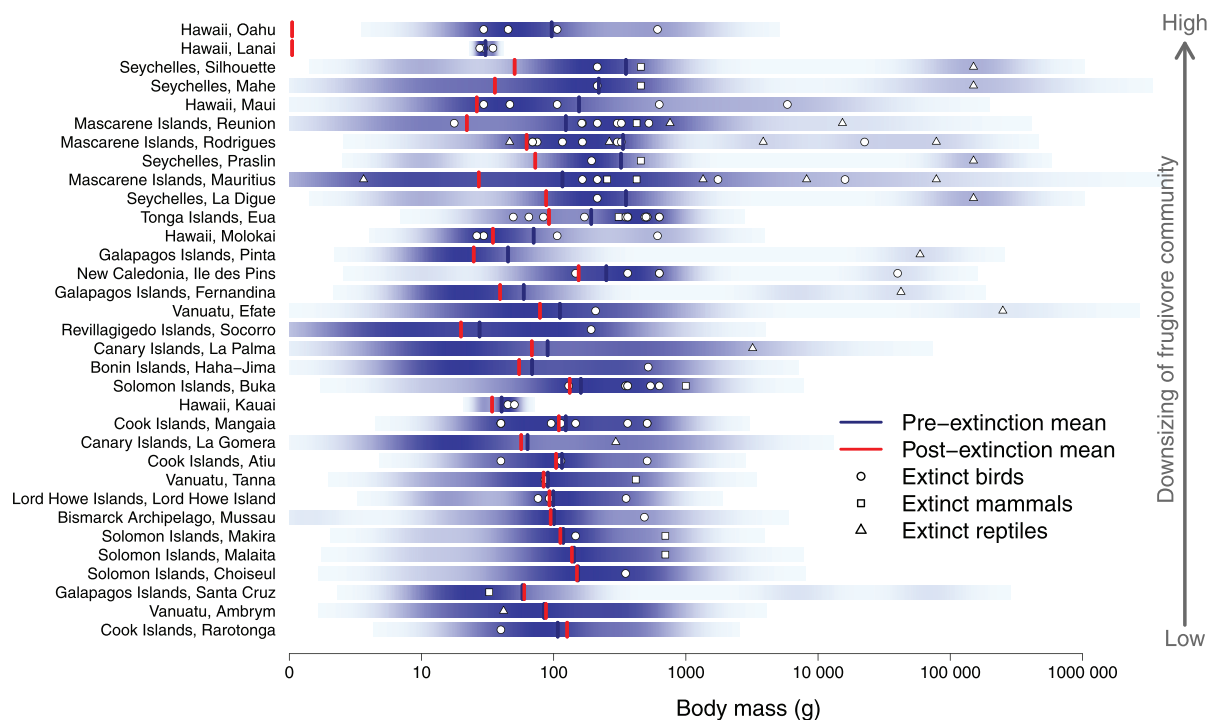


Figure 4. Extinction-driven downsizing of frugivore communities. Changes in community-level body mass of frugivores (birds, mammals, reptiles) are shown for 33 islands on which frugivore extinctions have occurred. For each island, the body mass frequency distribution before extinction is indicated with blue density strips (dark blue = high density of species with a particular body mass, light blue = low density). The pre-extinction mean body mass (dark blue dash) and the post-extinction mean body mass (red dash) are illustrated for each community. The body masses of extinct bird species (circles), mammals (squares) and reptiles (triangles) are indicated for each community. Islands are sorted according to the amount of change in mean community-level body mass (grey arrow) indicating the magnitude of downsizing of frugivore communities.

that a pervasive ecological downsizing of insular frugivore communities has occurred due to the predominant loss of large-bodied vertebrates. We suspect that this has serious consequences for insular plant populations and ecosystems.

Magnitude and geographical distribution of insular frugivore extinctions

Previous community-level studies of insular extinctions across multiple archipelagos have usually focused on birds (Blackburn et al. 2004, Duncan et al. 2013, Boyer and Jetz 2014). Instead, our analysis summarizes insular frugivore extinctions across all three vertebrate classes (birds, mammals and reptiles). Although birds represent the majority of frugivore species on islands, reptiles such as lizards (Olesen and Valido 2003) and tortoises (Hansen and Galetti 2009) as well as mammals such as frugivorous bats (Whittaker and Jones 1994) also play a key role for animal-mediated seed dispersal on islands (Kaiser-Bunbury et al. 2010). Within some archipelagos (e.g. Galapagos, the Mascarenes, Comoros, Canary Islands and Solomon Islands), reptiles or mammals are relatively more diverse than in other archipelagos (Supplementary material Appendix 6). This suggests that the relative importance of particular vertebrate classes for animal-mediated seed dispersal and their

role for ecological functioning varies geographically among archipelagos.

Many islands have lost large proportions of their original frugivore communities, with some islands (e.g. within Hawaii, the Cook Islands, Tonga Islands, the Mascarenes and the Seychelles) having lost > 50% of their pre-extinction frugivore richness. Especially the Pacific region – following waves of extinctions after both pre-European and European colonization – has seen one of the largest extinction events in the Holocene (Steadman 2006, Boyer 2008, Duncan et al. 2013). Our results further show high proportional extinctions in other parts of the world such as the Indian Ocean (Mascarenes and Seychelles). For instance, in the Mascarenes at least 30 frugivores became extinct (18 birds, 2 mammals, 10 reptiles), including the dodo *Raphus cucullatus*, the Mauritian giant skink *Leiolopisma mauritiana* and giant tortoises *Cylindraspis* spp. This suggests a dramatic loss of ecological function relative to pre-human native ecosystems (Rijsdijk et al. 2009, Kaiser-Bunbury et al. 2010) and severe consequences for insular seed-dispersal networks (Schleuning et al. 2014).

Extinction and island characteristics

Our analysis of island characteristics revealed that distance to the mainland, island area and maximum elevation were the

three strongest correlates of proportional extinction. Proportional extinction was highest on isolated and small islands and increased with island elevation. Larger areas allow more species to coexist than smaller areas (Arrhenius 1921), e.g. due to reduced extinction rates (MacArthur and Wilson 1967). Moreover, because resources are limited on small islands, human-induced habitat loss, hunting and invasive species can quickly affect the whole island (Whittaker and Fernandez-Palacios 2007). For the positive effect of distance to the mainland, we suggest that island isolation often causes exaggerated ecological release, resulting in evolutionary modifications such as gigantism and flightlessness (MacArthur and Wilson 1967, Lomolino et al. 2010). Such traits can make species particularly prone to extinction. The positive effect of maximum elevation (as similarly found in Blackburn et al. 2004) is unexpected and might be explained by species being restricted to small areas of suitable habitat along the elevational gradient, making them more vulnerable to extinction if this is lost.

Precipitation, temperature and surrounding landmass proportion did not show a statistically significant effect on proportional extinction of frugivores. Precipitation and temperature might play a minor role in our study because all islands are located within the (sub-)tropics and the oceanic climate around islands might have a buffering effect (Cronk 1997, Kissling et al. 2012). Surrounding landmass proportion, a good predictor of plant species richness on islands (Weigelt and Kreft 2013), might have been unimportant in our GLMMs because we used archipelago as a random effect, which probably captures most of the spatial variation in land masses around islands. Moreover, it is important to note that variation among archipelagos dominated in explaining proportional extinction compared to the effects of single island characteristics. This suggests that additional factors at the archipelago level – such as human arrival time – are required to more fully explain insular extinctions worldwide.

Traits and extinction probability

Extinction probability of frugivores was strongly linked to species' traits. As previously observed for insular bird communities (Steadman 2006, Boyer 2008, Duncan et al. 2013, Boyer and Jetz 2014), large and flightless species suffered higher rates of extinction than did small-bodied and volant species. This substantiates that the loss of species is not a random but a selective process, where specific intrinsic traits lead to high vulnerability (McKinney 1997, Cardillo et al. 2005, Eskildsen et al. 2015). Large-bodied frugivores are particularly prone to extinction because their space use and resource requirements increase with increasing body size (Haskell et al. 2002), and hence large frugivores are much more sensitive to small areas than small frugivores are (Sodhi et al. 2004, Boyer and Jetz 2010). The loss of large-bodied vertebrates is ubiquitous across the globe and can have far-reaching consequences for ecosystem processes (Estes et al. 2011), including negative effects on plant regeneration and seedling recruitment (Meehan et al. 2002,

Galetti et al. 2013, Pérez-Méndez et al. 2015, 2016). Flightless species are extinction prone because they are vulnerable to hunting, habitat loss and exotic predatory mammals which were often established on islands after European colonization (Blackburn et al. 2004, Steadman 2006, Boyer 2008, Duncan et al. 2013).

Downsizing and changes in community-level body mass

Our results revealed a substantial ecological downsizing of many insular frugivore communities worldwide. Across the 33 islands that have recorded extinction events, post-extinction changes in body size were predominantly characterized by a community-wide reduction (mean: 37%; range: –18–100%), often losing the largest frugivore. Such ecological downsizing can entail the loss of unique ecological functions (Boyer and Jetz 2014) and negatively affect seed dispersal, gene flow and recruitment of plants (Meehan et al. 2002, Pérez-Méndez et al. 2015, 2016).

The actual consequences of frugivore extinctions for plant regeneration and ecosystem dynamics on islands have yet been little studied. Large-bodied frugivores are disproportionately important as dispersers because they can swallow or handle large fruits and deposit seeds far away from the parent plant (Blake et al. 2012, Wotton and Kelly 2012). For two large-seeded New Zealand tree species, field experiments suggest that dispersal failure reduces plant regeneration through effects on seed predation, germination and seedling survival (Wotton and Kelly 2011). In the Canarian archipelago, the extinction of large-bodied lizards (*Gallotia*, Lacertidae) has led to a strong reduction of seedling recruitment (Pérez-Méndez et al. 2015) and gene flow (Pérez-Méndez et al. 2016) in plants that rely exclusively on lizards for seed dispersal. On Galapagos, the presence of giant tortoises (genus *Geochelone*) facilitates a greater recruitment of an arboreal cactus which is an important keystone resource for many other animals (Gibbs et al. 2008). These examples highlight the important consequences of insular frugivore extinctions for trophic interactions, but more studies are clearly needed to better quantify the effects of ecological downsizing on plant regeneration and ecosystem dynamics, especially on islands (Hansen and Galetti 2009).

Implications for conservation and restoration

Our results provide several implications for the conservation and restoration of island ecosystems. While we acknowledge that the (sub-)fossil record is incomplete and can be biased towards particular regions, taxa or size classes (Steadman 2006, Boyer 2008, Duncan et al. 2013, Kemp and Hadly 2015), our data provide a first comparative baseline for preserving and restoring plant–frugivore interactions on many islands. The underlying dataset (available from the Dryad Digital Repository) allows to identify particular frugivores and their ecological function (e.g. approximated by traits such as body size) in the context of pre-extinction communities.

This can facilitate the restoration of native seed dispersal interactions, e.g. by increasing populations of functionally unique species or by replacing extinct species with taxon substitutes (Kaiser-Bunbury et al. 2010). The latter approach, rewilding of ecosystems by introducing extant species as functional replacements or ecological analogues for extinct native species, is controversial but gaining momentum given the need to remedy defaunation and restore trophic cascades in the Anthropocene (Svenning et al. 2016), including on islands (Kaiser-Bunbury et al. 2010). Conservation practitioners are starting to employ large and giant tortoises (family Testudinidae) in island ecosystems such as the Galapagos, the Mascarenes and the Seychelles to replace extinct tortoises with extant analogues (Hansen et al. 2010). This can improve seed germination and establishment of endangered large-fruited plant species (Griffiths et al. 2011). However, implementation of rewilding projects to restore plant–frugivore interactions on islands is still rare (Kaiser-Bunbury et al. 2010), and empirical evidence as well as rigorous scientific studies on trophic rewilding are often lacking (Svenning et al. 2016).

Conclusion

Our study synthesizes current knowledge of extant and extinct frugivorous vertebrate species and documents widespread extinctions and pervasive ecological downsizing on many islands. Two key conclusions can be drawn. From a scientific point of view, our findings encourage predictions of extinction risks by demonstrating that large and flightless species on small and isolated islands are most prone to extinction. The models that were built in this study provide an important building block for forecasting the likely effects of future global change on biodiversity because both extrinsic factors (e.g. island characteristics) and intrinsic traits (e.g. body size and inability to fly) emerge as key predictors of extinction risk. From a conservation perspective, our results suggest that targeted conservation and rewilding efforts on islands are urgently needed to halt the defaunation of large and non-volant seed dispersers and the trophic downgrading of insular frugivore communities. This requires empirical studies on the ecological consequences of insular frugivore extinctions and how to restore functional (mega)faunas and extinct interactions within island ecosystems.

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Supplementary material (Appendix ECOG-03462 at <www.ecography.org/appendix/ecog-03462>). Appendix 1–6.